

SYSTEMATIC RESOLUTION OF THE GENERA OF THE *CRINIA* COMPLEX (AMPHIBIA: ANURA: MYOBATRACHIDAE)

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Abstract.—Re-evaluation of morphological analyses and generic taxonomy of Australian myobatrachine frogs in the *Crinia* complex is undertaken in light of new genetic data. All species currently in the genera *Ranidella* and *Crinia* are assigned to *Crinia*. The genera *Paracrinia* and *Geocrinia* are retained.

Four Australian genera, *Ranidella*, *Crinia*, *Paracrinia*, and *Geocrinia* (Myobatrachidae: Myobatrachinae), collectively designated the “*Crinia* complex,” comprise a group of small, rather nondescript frogs (Heyer & Liem 1976). The species of this complex have been partitioned into genera by recent authors with differing results. All recent authors agree concerning the smallest groups of species clusters in this complex, but considerable disagreement exists regarding the assignment of these groups at the generic level. Currently hypothesized groups and classifications are summarized in Table 1.

The following morphological and behavioral characters differentiate the species clusters: vomer and vomerine teeth, omohyoideus muscle, outer metatarsal tubercle, belly texture, egg placement, and mating call. However, clustering algorithms provide no unequivocal pattern of relationships among these species: “There is no way to group the . . . taxa so that two of the derived states of these characters define the same assemblage. Rather, a grouping which results in a cluster having all the taxa with the same derived state of one character leads to convergence of states in the other characters” (Heyer and Liem 1976:9). Thus, the data presented by Heyer and Liem (1976) are certainly open to alternate clustering interpretations than theirs. The phenetic analyses of Blake (1973) and Thompson (1981) recognize the same basic species groups, but the clustering pattern of the groups was highly variable dependent on data scoring and the algorithm used. Within the *Crinia* complex, morphological variation is so limited that it has been impossible to achieve a stable clustering scheme and, hence, taxonomic consensus. For these cases where the nature of the morphological data preclude a definitive analysis of relationships, use of a different data base is required for analysis of relationships.

Daugherty and Maxson (in press) recently estimated genetic relationships among species of the *Crinia* complex based on MC’F (micro-complement fixation) data from the serum protein albumin. These genetic data, in concert with the morphological data, provide a new basis for determining evolutionary lineages within the complex. The major lineages are herein proposed as generic units in order to provide a stable classification for this complex.

The Genetic Data

Immunological distances derived from comparisons of serum albumins provide both cladistic information and a time framework for interpreting evolutionary

Table 1.—Species clusters and generic assignment of the *Crinia* complex.

	Blake, 1973	Heyer & Liem, 1976	Thompson, 1981	This study
<i>georgiana</i>	Together with <i>haswelli</i> , <i>Crinia</i>	<i>Crinia</i>	Not studied	<i>Crinia</i>
<i>haswelli</i>	Together with <i>georgiana</i> , <i>Crinia</i>	<i>Paracrinia</i>	Not studied	<i>Paracrinia</i>
<i>laevis</i> cluster	<i>Geocrinia</i>	<i>Geocrinia</i>	Not studied	<i>Geocrinia</i>
<i>signifera</i> cluster	Species group of <i>Ranidella</i>	<i>Ranidella</i>	Distinct species group of <i>Ranidella</i>	<i>Crinia</i>
<i>riparia</i>	Together with <i>tasmaniensis</i> , second species group of <i>Ranidella</i>	Together with <i>tasmaniensis</i> , <i>Australocrinia</i>	Second distinct species group of <i>Ranidella</i>	<i>Crinia</i>
<i>tasmaniensis</i>	Together with <i>riparia</i> , second species group of <i>Ranidella</i>	Together with <i>riparia</i> , <i>Australocrinia</i>	Third distinct species group of <i>Ranidella</i>	<i>Crinia</i>

relationships. In the past decade, such protein data have been used extensively in phylogenetic studies of diverse amphibian taxa (e.g., Heyer and Maxson 1982; Maxson 1981). Albumin immunological distances (ID) have been shown to estimate sequence differences in albumins between species (Maxson and Wilson 1974) and to accumulate measurable sequence differences at an approximate rate of one substitution per lineage per million years (Wilson *et al.* 1977). Daugherty and Maxson (in press) have measured a series of immunological distances among the albumins of many members of the *Crinia* complex. The data consist of one-way comparisons to *signifera*, currently assigned to the genus *Ranidella* (Table 2). The pattern of divergence from *signifera* reveals the major genetic lineages within this complex.

Members of the *signifera* cluster (Table 2) exhibit ID values ranging from 24 to 40. The distance to *riparia* is 15 units and to *tasmaniensis* is 53 units. Clearly, *riparia* belongs to the same genetic lineage as other members of the *signifera* cluster. The ID value for *tasmaniensis* is somewhat higher than values measured to members of the *signifera* group, but not as large as values to other lineages (*haswelli* and *laevis*; see below) within the *Crinia* complex. Furthermore, an ID value of around 50 is often seen between species within other frog genera (e.g., Maxson and Wilson 1975; Heyer and Maxson 1981). The immunological evidence thus supports Thompson's (1981) proposal that *Australocrinia* (i.e., *riparia* and *tasmaniensis*) be synonymized with *Ranidella* (i.e., the *signifera* cluster).

The ID to *georgiana* is 29 units, suggesting that *georgiana* is part of the same genetic lineage as the frogs in the *signifera* cluster. For both *georgiana* and *riparia*, the ID values to *signifera* are smaller than most ID values measured between *signifera* and other members of the *signifera* group. The taxonomic

Table 2.—Albumin immunological distances between *signifera* and other species of the *Crinia* complex.*

Species compared	ID to <i>signifera</i>
<i>signifera</i> cluster:	
<i>signifera</i>	0
<i>glauerti</i>	24
<i>parinsignifera</i>	24
<i>bilingua</i>	30
sp. nov.	31
<i>remota</i>	31
<i>deserticola</i>	40
<i>riparia</i>	15
<i>tasmaniensis</i>	53
<i>georgiana</i>	29
<i>victoriana</i>	133
<i>haswelli</i>	140

* Data from Daugherty and Maxson (in press).

conclusions are that *Ranidella* (including *Australocrinia*) and *Crinia* are congeneric and that *Ranidella* is a synonym of *Crinia*.

On the other hand, the ID value of *signifera* to *victoriana*, the only member of the *laevis* group tested to date, is 133. This very large value is concordant with recognition of the genus *Geocrinia*. The ID of *signifera* to *haswelli* is similarly high, 140. The similar, but high, ID values of *haswelli* and *victoriana* to *signifera* indicate a distant relationship of *haswelli* and *victoriana* to *signifera*. The values do not indicate what the relationship of *haswelli* is to *victoriana*; it could be close or distant. In fact, preliminary data (Maxson and Daugherty, unpublished) indicate a distant relationship between those taxa (ID value between 90 and 100). These data are consistent with recognition of the genera *Geocrinia* (including *victoriana*) and *Paracrinia* (including *haswelli*).

Discussion

Several conclusions regarding evolution of the *Crinia* complex logically follow from recognition of the genera *Crinia*, *Geocrinia*, and *Paracrinia*.

Several of the character states that differentiate among the species clusters have apparently evolved independently several times. Loss of the vomer and vomerine teeth has occurred within both *Crinia* and *Geocrinia*. Both smooth and granular bellied frogs occur in the genus *Crinia*. All major variation in mating call occurs within the genus *Crinia*. Perhaps most notable is that variations in life history occur within, rather than among lineages. The change from a lotic to lentic egg placement and larval morphology has taken place entirely within the genus *Crinia*, and these life history differences cannot be used to define generic units. A similar situation occurs within the genus *Geocrinia*, with evolution of terrestrial larvae from pond larvae.

The morphological characters that differentiate among the genetically defined lineages are, for the most part, characters involving reduction or loss as the derived state. *Crinia* species have an outer metatarsal tubercle; *Geocrinia* species

lack the tubercle. *Crinia* species have an omohyoideus muscle; *Paracrinia* lacks the muscle. *Geocrinia* species lack an outer metatarsal tubercle and toe fringing; *Paracrinia* has a metatarsal tubercle and toe fringing. Of these characters, the only one that does not involve reduction or loss as the derived state is the metatarsal tubercle (Heyer and Liem 1976).

Derived states involving reduction or loss are usually considered to contain little or no phyletic information (Hecht and Edwards 1976). That morphological states of loss or reduction are the primary criteria permitting morphological discrimination of the genera within the *Crinia* complex (which the genetic data show to be greatly differentiated) suggests that the use in systematics of characters of loss and reduction needs re-evaluation. It also further documents the extreme morphological conservatism so often observed in anuran evolution (Maxson and Wilson 1975; Wilson *et al.*, 1977) and reinforces the need to examine genetic and other categories of characters when conducting phylogenetic studies (Blake 1973).

Generic Redefinition

Crinia is the only genus requiring redefinition. The format used is comparable to that of Heyer and Liem (1976), which may be referred to for definitions of the genera *Geocrinia* and *Paracrinia*.

Crinia Tschudi, 1838

Synonyms.—*Ranidella* Girard, 1853
 Camariolus Peters, 1863
 Pterophrynus Lutken, 1863
 Pterophryne Gunther, 1867
 Australocrinia Heyer and Liem, 1976.

Type species.—*Crinia georgiana* Tschudi, 1838.

Diagnosis.—A myobatrachine genus; cervical cotyles widely separated; vomer and vomerine teeth present or absent; narrow sacral diapophyses; depressor mandibulae muscle with or lacking a slip from the dorsal fascia; omohyoideus muscle present; tympanum present; belly smooth or granular; toes with or without fringe; outer metatarsal tubercle present; eggs placed in water or on land; pond or stream larvae.

Content.—*Crinia bilingua*, *deserticola*, *georgiana*, *glauerti*, *insignifera*, *parinsignifera*, *pseudinsignifera*, *remota*, *riparia*, *signifera*, perhaps *sloanei* (see Thompson 1981), *subinsignifera*, *tasmaniensis*, *tinnula*, and undescribed species. Present knowledge of variation within this genus (as here defined) does not support the recognition of species groups (also see Daugherty and Maxson, in press).

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